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Studies on larval nematodes parasitic in *Tubificidae*
(A hypothesis on the life-cycle of *Rhabdochonidae*)

Badania nad larwalnymi nicieniami pasożytującymi u *Tubificidae*
(Hipoteza cyklu rozwojowego *Rhabdochonidae*)

While studying parasites living in the oligochaete family of *Tubificidae* I found in the body cavity of *Tubifex tubifex* Müll. and of *Limnodrilus hoffmeisteri* Clap. very small Nematode larvae (Fig. 1a). The structure of the larva is typical of the suborder *Spirurata* Railliet and resembles that of the family *Rhabdochonidae* Skrjabin 1946.

The larva is 210—270 μ long. It has a well developed digestive tract typical of the *Spirurata*. The chitinous, brown-coloured pharynx is funnel-shaped and is slightly expanded at the base of the muscular oesophagus. The muscular oesophagus continues into the longer glandular oesophagus. The intestine is sharply marked off from the glandular oesophagus. The ratio of length of the oesophagus to the intestine is characteristic of larvae of the II-nd developmental stage the intestine being much shorter than the oesophagus quite contrary to the ratio prevailing in mature individuals of more advanced larval stages. The peripharyngeal nervous ring is plainly visible. In larvae fixed and stained with haematoxylin clusters of numerous deeply staining nuclei are visible above and below the nervous ring (Fig. 1b). The genital organs are undeveloped. The structure of the digestive tract i. e. the mentioned length ratio of its parts, the primitive chitinous funnel along with the complete lack of the gonads allow to classify the larvae as belonging to the II-nd developmental stage.

Measurements of larva

Length of body 210—270 μ
Length of pharynx 24 μ

Length of oesophagus 135 μ
Length of intestine 60 μ

In *Tubifex tubifex* I found the larvae mostly near the postgonadal segments. In *Limnodrilus* I found a single larva and that in the gonadal segment when dissecting the seminal vesicle in search of *Archigetes appendiculatus* which is parasitic there. The degree

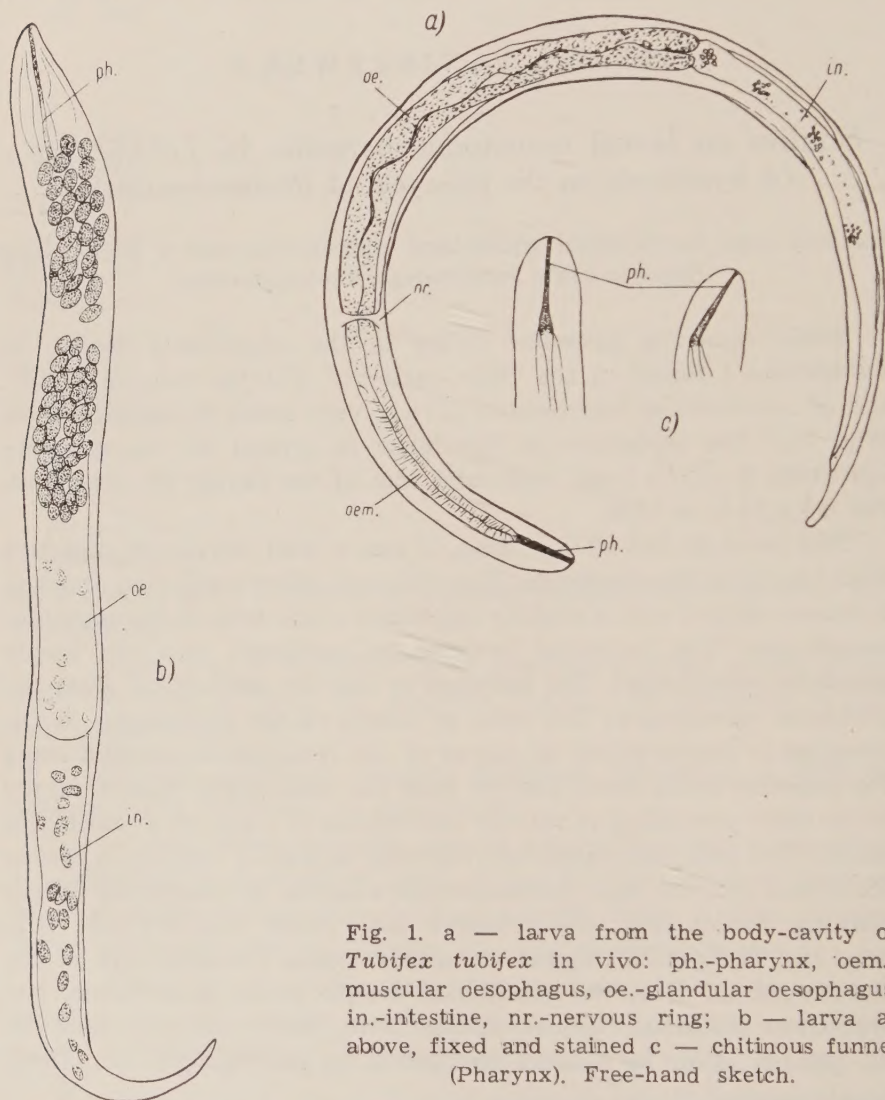


Fig. 1. a — larva from the body-cavity of *Tubifex tubifex* in vivo: ph.-pharynx, oem.-muscular oesophagus, oe.-glandular oesophagus, in.-intestine, nr.-nervous ring; b — larva as above, fixed and stained c — chitinous funnel (Pharynx). Free-hand sketch.

of infestation of the *Tubifices* was only slight: 1-4 larvae in one host. The larvae are free in the body cavity and are mostly spirally twisted. Because of their minute size and the slight degree of

infestation they are detected only with difficulty. Some of the infested *Tubifices* showed signs of heightened lymphocytosis. Larvae extracted from the host live in water for some twenty-odd hours moving about vigorously. They stain vitally with methylene-blue. With the chitinous funnel of their pharynx they execute movements reminiscent of nipping, but the pharynx is stiff and does not bend, moving only sideways (Fig. 1c). The pharynx is moved by special muscles which are clearly visible when in motion.

A hypothesis on the development of the larvae
of the *Rhabdochonidae* Skrjabin 1946

The infested *Tubificidae* came from the inundation areas of the rivers Odra near Wrocław and Ropa near Gorlice. What further hosts may these parasitic larvae have? Only Vertebrates feeding on Oligochaetes can come into account and among those, fish which eat the *Tubificidae* as e. g. *Barbus barbus* and *B. petenyi*. In the last named fish species, in specimens caught in the same localities as the infested *Tubificidae* I found the *Rhabdochonoides barbi* Janiszewski 1954, and therefore I venture the supposition that the larvae are developmental stages of this parasite. A further development leading to maturity and oviposition would take place in the gut of the fish.

Both T. H. Weller (1938) and P. V. Gustafson (1939 and 1942) carried the experimental studies concerning the life-cycle of *Rhabdochona*.

T. H. Weller placed the eggs of *Rhabdochona ovifilamenta* together with *Gammarus* sp., *Hyaella knickerbockeri* and larvae of some undescribed *Chironomidae*. It was observed that only *Hyaella knickerbockeri* was infested; in its intestine he found 9 motile larvae. Each larva had a chitinous stylet inside its mouth. As it is visible from the drawing the intestine of the larva consists of the sections typical for *Rhabdochona*. There is an obvious resemblance to the larva which I described formerly.

P. V. Gustafson stated in his short announcement (1939) that he found it experimentally that larvae of mayfly *Hexagenia*, *Heptagenia* and *Streptonoura* ate eggs of the *Spinitectus*, eggs of the *Rhabdochona* were eaten by larvae of the *Hexagenia*. All those eggs spread out in the intestine of the larvae within twelve hours and after three days they were visible in the body cavity. Then the infested mayfly were consumed by certain fish where further development of the larvae followed afterwards. In 1942 he repeated his experiments. He noticed some interesting cases, namely larvae of certain *Rhabdochona* sp. grew and developed further in various mayfly nymphs,

but there was noticeable a precocious maturity of the parasites. It had never been affirmed before that prematurity could affect that particular group of parasites.

From those experiments one can gather that the larvae of mayfly are intermediate hosts of the *Rhabdochonidae*. That does not exclude, however, that *Tubificidae* might be the intermediate hosts as well as the larvae of mayfly.

There are known some species amidst the *Spiruroidea*, which can develop inside the intermediate hosts belonging to different groups, for instance *Cheilospirura hamulosa* (Diesing 1851) can live in the *Amphipoda*, *Saltatoria* and *Coleoptera*; the *Tetrameres fissispina* (Diesing 1861) in the *Oligochaeta*, *Crustacea* (*Daphnia*, *Gammarus*), *Blatta* and *Saltatoria*.

Chabaud (1954) supposes that in the life-cycle of the *Spiruroidea*, the intermediate host — an invertebrate — is a comparatively new achievement and does not possess the phylogenetic specificity, i. e. adaptable to a certain group of hosts only. He assumes the *Arthropoda* are the intermediate hosts of the *Spiruroidea* with an exception of the *Tetrameres fissispina* which, according to Sugimoto and Nishiyama (1937), live in the *Annelida*, but it remains to be detected. In that case the *Tubificidae* would be another exception of that kind.

In the majority of cases the eggs of the *Rhabdochonidae* are provided with polar filaments though to a very variable degree. So for instance in some species of *Ascarophis* only two long filaments are present on one pole of the egg, in others there are two or even up to 10 filaments on both poles; *Rhabdochonoides barbi* Janisz. 1954 has 9—13 very long filaments whereas *Comephoronema verestschagini* Layman has many short and fine filaments. Without doubt all these are devices serving the purpose of locomotion of a passive kind as in planctonic organisms. If we admit that the bottom-dwelling *Oligochaetes* are intermediate hosts of the *Nematodes* as the previously described larvae seem to point at, then such devices would evidently be purposive. Being adaptations to the life conditions and the ethology of the slowly moving or semisedentary intermediate host they serve the distribution of the species.

The differences in structure and in properties of the eggs can doubtlessly be explained by the ecology and ethology of the intermediate host. Other parasites too living in *Tubificidae*, namely the Protozoans *Actinomyxidina* possess analogous adaptations for the

purpose of distribution of the species. The spores of the *Actinomyxidia* namely possess variously shaped processes of the triradially-symmetrical outer envelope. The bottom-dwelling Oligochaetes of the Tubificid family are a phylogenetically ancient groups as proved by their world wide distribution. The speciation of the parasite and the perfection of its adaptations took place simultaneously with the development and speciation of the host.

Among the *Spirurata* we find similar contrivances for the distribution of the species in *Tetrameres nouveli* (Seurat 1914) and *Tetrameres fissispina* (Diesing 1861) — *Tetrameridae* Travassos. Both species are parasitic in water-fowl and the last named has the Crustaceans *Daphnia pulex* and *Gammarus pulex* for intermediate hosts. Eggs of the *Hedrurinae* Railliet 1914 which are parasitic in fishes, amphibia and aquatic reptiles have a structure somewhat similar to the eggs of certain gnats (*Anopheles*) the eggshel being expanded round the equator and so the surface increased helping to float the egg. We know that some *Hedrurinae* have aquatic Crustacea for intermediate hosts (*Asellus aquaticus*).

Larvae of the *Spirurata* appear sometimes also encysted in the body-cavity of fishes. I discovered such larvae in *Pleuronectes flesus*, *Pleuronectes platessa* and *Gadus callarias* (Janiszewska 1939). They were however much larger and much more advanced in their development, so that they could be classed as larvae of the IIIrd stage. Their structure bears the characters of the *Rhabdochonidae*, they may belong to the genus *Ascarophis* van Beneden. The fishes in question were caught in coastal waters of the Baltic and in their gut I found among other food also *Tubificidae*.

Considering that the bottom-dwelling Oligochaetes (*Tubificidae*) are predominantly eaten by fishes and not by other Vertebrates and that the majority of fish parasites from the suborder *Spirurata* is embraced by the family *Rhabdochonidae* my supposition that larvae found by me belong to this family seems not to be unfounded. Definite proof can of course be brought only by experiments on infection which I intend to perform in the course of my further investigation.

On hand of the available data the hypothetical life-cycle of the *Rhabdochonidae* would present itself as follows: 1) Fishes feeding on minute bottom food among it on *Tubificidae* become infested by larvae of the IIInd stage. Some of these fishes as e. g. *Barbus barbus* and *B. petenyi* could thus become definitive hosts of the parasites.

2) Species parasitic in predatory fishes would need two intermediate hosts: Bottom-dwelling fauna i. e. Oligochaetes as a first intermediate host harbouring larvae of the IInd stage and some non-predatory fish feeding on bottom-dwelling fauna as a second intermediate or „depot” host. The larvae being unable to find adequate life-condition in the gut of these fishes would migrate into their body-cavity and encyst there in the shape of larvae of the IIIrd stage. Forms parasitic in the urinary bladder of fishes (*Cystidicola*) can be looked upon either as attempting such a migration or as showing a reminiscence of it.

The majority of species of the genera *Rhabdochona* Raillet, *Rhabdochonoides* Janiszewska, *Cystidicola* Fischer, *Meta-bronema* Yorke-Maplestone, *Comephoronema* Layman, *Sterliadochona* Skrjabin and others would in accordance with the scheme outlined above have a life-cycle including only one intermediate host. A life-cycle with two intermediate hosts would characterize *Ascarophis* van Beneden and others.

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STRESZCZENIE

Autorka opisuje larwę II stadium rozwojowego nicienia, pasożytującą w jamie ciała *Tubifex tubifex* Müll. i *Limnodrilus hoffmeisteri* Clap. Larwa wykazuje cechy budowy właściwe dla nicieni z rodziny *Rhabdochonidae* Skrjabin, podrzędu *Spirurata* Raillet. Autorka przypuszcza, że może to być larwa z rodzaju *Rhabdochona* Raillet lub *Rhabdochonoides* Janiszewska.

